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Functional Morphology: 'Point and Shoot' Prey Capture in Fishes

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The ability to protrude the jaws and capture elusive prey is a hallmark of fish evolution. New analyses provide insight into how jaw protrusion changed predator–prey relationships and fueled species diversification in ancient seas.

Energy acquisition is obviously of central importance to organismal survival, and as such it has long been held that features related to the ability to capture prey successfully are under strong selective pressure [1]. Nearly every aquatic vertebrate uses some suction for capturing prey, as well as processing (reducing the prey in some way) or transporting prey (moving it from the oral cavity into the esophagus) [2]. Even predators that use other modes of prey capture, namely ram (using forward locomotion to overtake the prey) or biting, typically require the use of suction in combination with one or both of these. Liem [3] posited that suction was used so prominently because of its inherent flexibility for capturing a wide variety of prey in the aquatic realm. He argued that the taxonomic and ecological diversity of prey that could be captured via suction by a single fish species was unsurpassed by any other mode of prey capture, aquatic or terrestrial, in the animal kingdom [3]. Jaw protrusion — the ability to project the upper jaws anteriorly, away from the head — is inherently linked to the generation of suction and has been credited with fueling much of the evolutionary success of the fishes as a group [4]. However, up to now, there remained no clear understanding of specifically how this trait played such an important role. In a new paper in this issue of *Current Biology*, David Bellwood and co-authors [5] provide compelling evidence that during the late Cretaceous (beginning ~100 million years ago), multiple clades of fish evolved jaw protrusion independently, or convergently, and potentially replaced other clades.

Convergent evolution refers to distantly related organisms reaching similar functional solutions to an ecological problem. The ecological 'problem', in this case, is feeding in the aquatic realm. Water is dense and viscous. If a predator

swims forward to overtake a prey item, they will very likely push the prey away by the 'bow wave' that is created as the predator moves through the water. Suction generation is perhaps the most common solution to this problem, at least among extant fishes [1,3].

Upper jaw protrusion plays several important and complementary roles during suction feeding. During suction feeding, fishes or other aquatic vertebrates rapidly expand the head to draw water into the open mouth [1], hopefully entrapping a prey item in that flow of water. Jaw protrusion is thought to both increase and direct the forces produced during suction generation [6–8], thereby increasing the changes of successfully capturing a prey item. Upper jaw protrusion reduces the gap between predator and prey more stealthily than whole body locomotion [9], which is essential, as suction works only over a very limited distance [10]. Increased jaw protrusion is positively correlated with an increase in elusive prey in the diet, such as fishes and shrimp [11]. Thus, jaw protrusion is tightly associated with the ability to forage more effectively in the aquatic realm.

Bellwood and co-authors [5] suggest a 'functional rearrangement' of clades favoring those with jaw protrusion and leading to the dominance of this trait among marine acanthomorph fishes (the 'spiny-rayed' fishes, which represent about 1/3 of all known fish biodiversity), as well as the appearance of the trait in freshwater, non-acanthomorph fishes. Over evolutionary time, the amount that the jaws were protruded also increased, meaning the fishes alive during a given period were able to protrude the jaws farther than fishes alive during earlier periods. Increased protrusion means, in theory, an increased ability to generate suction and/or an increased reliance on suction for prey capture.

In a fish without protrusion, the lower jaw rotates ventrally to create a 'V'-shaped mouth opening for prey capture (Figure 1A). However, in those species with protrusion, the upper jaw contains a mobile element formed by the paired (right and left) premaxilla bones that protrude toward the food during prey capture. Each premaxilla is shaped like an 'L', and the two extensions are termed the ascending and descending (or dentigerous) processes, respectively; Figure 1B). In most cases, when the premaxillae are protruded, the ascending process slides along the nasal elements of the neurocranium, and as such there is something of a track for guiding and/or constraining protrusion and retraction [4]. As the premaxillae are protruded, the sides of the open mouth are occluded and a more tubular mouth opening is formed. This leads to the aforementioned advantages for prey capture and suction generation.

Bellwood and co-authors [5] used this basic morphological information to predict the protrusion ability of fossil fishes. Because of the way that the ascending process guides or constrains protrusion, the length of the ascending process of the premaxilla is thought to be a reasonable predictor of protrusion [4]. Bellwood and co-authors [5] tested the validity of this metric for predicting jaw protrusion ability. For any metric to work well, with precision and accuracy, the metric must map onto performance nearly perfectly, meaning a one-to-one match. To ensure this one-to-one matching of morphology with performance, Bellwood and co-authors [5] tested the match between ascending process length and observed jaw protrusion to a massive dataset of extant fish species from 37 families. A strong linear relationship was detected, providing the first ever verification of this metric for predicting performance.

For ancient fishes, jaw protrusion undoubtedly changed the nature of predator–prey interactions. The rise of suction feeding represented a shift away from the biting mode of prey capture dominant within the placoderms [2]. The placoderms (placo = plate + derm = skin) were among the earliest jawed fishes, with heavily armored heads. Known primarily from the Devonian (beginning ~400 million years ago), these are now extinct and known only from fossils. Anderson and Westneat [12] used engineering principles (aka four-bar linkages) to estimate the forces produced during biting in *Dunkleosteus*, an exceptionally large and formidable placoderm. By inputting movement parameters gathered from extant species, they predicted that a 1000 kg *Dunkleosteus* specimen had one of the most forceful bites of any known vertebrate, on the order of 4000–5000 N. *Dunkleosteus* has large jaw closing muscles (adductors), and a jaw with a high mechanical advantage, which amplifies the forces produced by the adductor muscles [12]. While this is impressive, and quite effective for gaining access to physically defended prey (such as with armor or hard shells), a shift away from biting afforded predators more flexibility in terms of the kinds of food they could successfully capture [3].

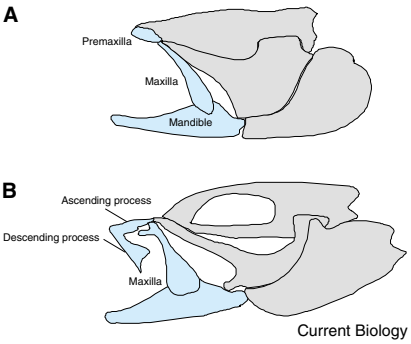

Figure 1. Mechanism of jaw protrusion in fishes.
Stylized images of a typical non-acanthomorph fish incapable of jaw protrusion (i.e., salmon) (A), and a typical acanthomorph fish capable of protrusion (B). The maxilla + premaxilla (or upper jaw), and mandible (or lower jaw) are shaded in blue. In (B), the maxilla is mobile, which can help to occlude the sides of the open mouth, but 'upper jaw protrusion' refers almost exclusively to the anteriorly directed motion of the premaxilla. Images modified after [4] by permission of Oxford University Press.

While upper jaw protrusion is not the only way to enhance suction production, it is a dominant mechanism among fishes as a whole, including chondrichthyans (sharks and rays) and chondrosteans (sturgeon). In all cases, the ability to protrude the jaws facilitates getting closer to the prey, where suction is effective, and to overcome prey defenses such as speed, crypsis, and hiding. This ability has increased the complexity of species interactions, potentially fueling whole new levels of predator–prey arms races. It is, therefore, not surprising that this innovation has evolved over and over again [2]. Jaw protrusion, quite literally, changed the face of fishes feeding in the aquatic realm.

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Reproductive Evolution: Pulling the Plug on Selection

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Hermaphroditism leads to reduced sexual selection and can result in the retention of deleterious mutations. A new study characterizes one such mutation that results in male–male copulation in nematodes, while also implicating a previously undescribed source of chemical signaling.

> *"If all the matter in the universe except the nematodes were swept away, our world would still be dimly recognizable […] we would find its mountains, hills, valleys, rivers, lakes and oceans represented by a film of nematodes."*
>
> Nathan Augustus Cobb, Nematodes and their relationships, 1914

Within the animal kingdom, mating is a competitive and consistent aspect of life. Success of mating is essential for passing on of genes and for genetic diversity. Sexual reproduction generally entails mating between a male and a female. However, there are species in which a single individual can exhibit both male and female characteristics. These organisms, known as hermaphrodites, have the ability to reproduce through self-fertilization. Due to lack of genetic diversity in the hermaphroditic mating system harmful mutations may persist within populations. Therefore, hermaphroditism, or 'androdioecy' (populations consisting of males and hermaphrodites), results in a decreased ability to respond to selection [1]. In this issue of *Current Biology*, a new study in nematodes by Noble *et al.* [2] details a unique genetic locus that persists due to the advent of this androdioecy.

Nematodes, or 'roundworms', inhabit a variety of ecological niches around the world, making them one of the most widespread phyla on the planet. Most nematodes are free-living, but some are parasitic on both animals (including humans) and plants. Nematodes are considered to be eutelic — every individual of a given species contains the same number of cell nuclei, in the same position within the body. Just like other animals, most nematode species are gonochoristic, meaning the species is comprised of both males and females. However, there are certain nematode species that comprise both hermaphrodites and males [3,4]. Though nematode hermaphrodites look like females morphologically, their initial germ cells give rise to sperm, which are stored in a specialized structure called the 'spermatheca'. The germ cells produced later in development form the eggs, and sperm from the spermatheca are used to fertilize these mature oocytes. Hermaphrodites cannot copulate with other hermaphrodites, but they do have the additional ability to copulate with males in order to produce cross-progeny, or offspring with diversified genetics.

Hermaphroditism is viewed to be common in nematodes due to the large body of work in the genetic model system *Caenorhabditis elegans*. However, it is important to note that only three species within the *Caenorhabditis* genus — *C. elegans*, *C. briggsae*, *and C. tropicalis* — have evolved this trait, and they have all evolved it independently [5,6]. Most *Caenorhabditis* species are in fact

